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## Original investigation

# Assessing competition between forest rodents in a fragmented landscape of midwestern USA

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## Abstract

Forests of the agricultural midwestern United States are highly fragmented, and species of small mammals that rely on the remaining forest fragments exhibit non-random distributions. We tested the extent to which interspecific competition between pairs of five species of granivorous forest rodents has influenced the structure of local assemblages occupying forest patches. We used a regression technique and incorporated patch and landscape variables in addition to local habitat variables. After accounting for variation in focal species density explained solely by local habitat variables, significant levels of interspecific competition were implicated for *Sciurus niger*–*Tamias striatus*. *T. striatus* also had a negative effect on densities of *Peromyscus leucopus* in forest patches > 10 ha. Inclusion of patch and landscape variables increased the explanatory power of regressions for *T. striatus* and *S. carolinensis*, two species generally regarded as sensitive to agriculturally induced fragmentation of forest habitat. Even when allowing for habitat selection at larger spatial scales, our results indicated competitive effects comparable to the analysis incorporating only local habitat variables. One difference was a marginal negative effect of *S. carolinensis* on *Tamiasciurus hudsonicus* after accounting for multi-scale selection. Overall, interspecific competition explained a significant proportion of the variation in densities for only three of the 24 potential interactions. In contrast, habitat and landscape features explained 0.37–0.71 of the variation in densities for all species except *S. niger* (0.09–0.20). We discuss the roles of competition and habitat fragmentation in mediating the coexistence of forest granivores.

**Key words:** Rodents, competition, fragmentation, habitat selection

## Introduction

Numerous studies have examined the degree to which interspecific competition influences the composition of communities (ABRAMS 1988; BENGTTSSON 1991; reviewed by CONNELL 1983; DRAKE 1990; HALLETT et al. 1983; MCINTOSH 1995; MINOT and PERINS 1986; NEE and MAY 1992; ROSENZWEIG

et al. 1984). In addition, studies of island biogeography (MACARTHUR and WILSON 1967) have shown that groups of insular faunas, resulting from either geological or anthropological processes, typically exhibit highly ordered (i. e., nested) patterns of species distribution (CUTLER 1994; MCCOY and

MUSHINSKY 1994; PATTERSON and ATMAR 1986; PATTERSON 1990; WRIGHT et al. 1998). Nested patterns of distribution often result from differential colonization and/or extinction probabilities among species (ATMAR and PATTERSON 1993; PATTERSON 1990). Factors influencing these colonization or extinction probabilities may include intrinsic characteristics of species such as minimum-area requirements, vagility, specific habitat affinities, and population stability (PATTERSON 1990; PELTONEN and HANSKI 1991).

In the absence of habitat fragmentation, differential habitat affinities of species can ameliorate competitive interactions, thus emphasizing the importance of considering local habitat effects in analyses of interspecific competition (ABRAMSKY et al. 1979; CROWELL and PIMM 1976; HALLETT et al. 1983). Theoretical models predict that habitat fragmentation may promote coexistence of competing species by permitting inferior competitors to escape spatially, even in the absence of differences in habitat affinities (ABRAMS 1988; HOLMES and WILSON 1998; HUXEL and HASTINGS 1998; MOILANEN and HANSKI, 1995; NEE and MAY 1992). Moreover, empirical evidence suggests that mammalian species select habitat at multiple spatial scales rather than just at local scales, and patch- and landscape-level selection can have important influences on community composition (LINDENMAYER et al. 1999, 2000; SCHWEIGER et al. 2000). In at least some instances local competition interacts with landscape-level habitat selection, influencing community structure (GABOR and HELLGREN 2000). Habitat selection by species at the local, patch and landscape-level may be a major mechanism structuring communities in fragmented landscapes; thus, it would be prudent to examine the importance of habitat structure measured at multiple spatial scales on populations before invoking competitive interactions as mechanisms structuring a community.

Our aim in the present study is to test for competition after incorporating habitat selection at multiple spatial scales rather than only at a single spatial scale. We focus our

tests on five species of granivorous forest rodents that occur syntopically in our study area in west-central Indiana, USA: white-footed mice (*Peromyscus leucopus*), eastern chipmunks (*Tamias striatus*), red squirrels (*Tamiasciurus hudsonicus*), gray squirrels (*Sciurus carolinensis*), and fox squirrels (*S. niger*). These species exhibit a highly nested distribution among forest patches in agricultural landscapes (NUPP and SWIHART 2000), but they vary considerably in the degree to which local, patch, and landscape features influence their density or distribution (NUPP 1997). In addition to our general tests for competition, we tested the hypothesis (NUPP and SWIHART 1996, 1998) that white-footed mice occupying smaller patches are released from interspecific competition in fragmented landscapes due to the absence of larger granivores. This test was accomplished by conducting separate analyses for mice in forest patches < 10 ha and  $\geq$  10 ha.

## Material and methods

### Study area

Our study was conducted on the Indian Pine Natural Resources Area in west-central Indiana. This 259 km<sup>2</sup> area encompasses two major watersheds in Tippecanoe and Warren counties; 82% of the landscape is subjected to cultivation, principally for production of corn and soybeans. Within this agricultural landscape, woodlands comprise 16% of the area and consist of small, more or less isolated farmland woodlots and larger wooded riparian strips (SHEPERD and SWIHART 1995). Thirty-five woodlots (0.1–150 ha) and two sites representative of more extensive wooded areas (~1500 ha) were selected for study based on the criteria of relatively mature, deciduous woody vegetation. These study sites were 30–870 m from their nearest neighboring forest patch.

### Determination of density

Each study site was sampled at least once during spring of 1992 to 1996 by live-trapping. Sherman<sup>tm</sup> live-traps (7.5 × 9.0 × 30 cm) were placed at 15-m intervals and Tomahawk<sup>tm</sup> live-traps

(15×15×60 cm) at 30-m intervals on sampling grids established at each study site. All traps were pre-baited for 2 days and followed by 5 days of trapping. Sherman traps were baited with a mixture of rolled oats, sunflower seeds and peanut butter, and Tomahawk traps were baited with English walnuts.

Abundance estimates of adult mice (> 18 g) (CUMMINGS and VESSEY 1994) were calculated using program CAPTURE (OTIS et al. 1978), and abundance of other adult small mammals (eastern chipmunks > 80 g, red squirrels > 200 g, gray squirrels > 400 g, and fox squirrels > 600 g) was estimated using minimum number known alive (MNA; Krebs 1966). Density estimates were calculated subsequently using either the entire area of woodlots (when the entire area was trapped) or the area of the trapping grid plus a 7.5-m buffer on all sides (for areas that were too large to cover completely, in which case a grid of ~2 ha was used).

### Quantification of habitat features

We used standard line transect and point-count sampling to quantify structural characteristics of the local habitat in each forest patch with 24 variables (Tab. 1). Parallel transects were spaced at 15-m intervals on trapping grids. Diameter at breast height (dbh) was measured for all trees > 10 cm and ≤ 1.5 m from a transect line. Trees also were classified as hard-mast (i. e., nut) producers, soft-mast (i. e., samara, fruit) producers, conifers, or other. Basal area, average dbh, and frequency were computed for all trees, snags, hard-mast producers (further separated into *Quercus*, *Carya*, and *Juglans*), soft-mast producers, and conifers. Counts of stumps, logs, grapevines, and burrows were obtained along transects and expressed in terms of their frequency per 100 m. At 30-m intervals along each transect, we measured vertical vegetative cover from 0–1 m, 1–2 m, and 2–3 m above ground using a modified density

**Table 1.** Habitat, patch, and landscape variables used in principal components analysis for detecting variation in granivorous rodent density as a function of habitat measured at multiple spatial scales. The acronym dbh refers to diameter at breast height. Total and sound mast production, as well as mast production excluding walnuts were used only in the analysis with 37 trapping episodes. Except for fractal dimension, patch and landscape variables were transformed using square roots (core area index) or natural logarithms (all other variables) before analysis. Squared terms, centered on mean values, also were included for patch area, proximity, and nearest neighbor distance. See text for details related to each variable.

Local Habitat Variables	Patch and Landscape Variables
Basal area of all trees	Area of forest patch
Basal area of hard-mast trees	Perimeter of forest patch
Basal area of oaks ( <i>Quercus</i> )	Core area index of patch
Basal area of hickories ( <i>Carya</i> )	Fractal dimension of patch
Basal area of walnuts ( <i>Juglans</i> )	Proximity of focal patch to other patches
Basal area of soft-mast trees	Distance to nearest neighboring patch
Basal area of conifers	
Basal area of snags	
Average dbh of hard-mast trees	
Average dbh of soft-mast trees	
Average dbh of snags	
Number of hard-mast trees	
Number of soft-mast trees	
Number of grapevines	
Number of snags	
Number of stumps	
Number of logs	
Vertical cover, 0–1 m	
Vertical cover, 1–2 m	
Vertical cover, 2–3 m	
Percent canopy cover	
Total mast production (kg/ha)	
Sound mast production (kg/ha)	
Mast production excluding walnuts (kg/ha)	

board (NUDDS 1977). Percent canopy closure was measured at 30-m intervals using a spherical densiometer (LEMMON 1957).

Previous studies have documented the importance of production of hard mast on population dynamics of white-footed mice, eastern chipmunks, and tree squirrels (e.g., MCSHEA 2000; NIXON et al. 1975; WOLFF 1996). Production of hard mast was estimated using seed traps placed at 30-m intervals within the trapping grids. Seed traps were constructed of circular plastic bags (1 m<sup>2</sup> area) elevated off the ground. Traps were placed before mast began to fall, in late August or early September of 1993, 1994, or 1995. Mast was collected from the traps in October, sorted by species and soundness, oven-dried, and weighed. Unfortunately, it was not possible to estimate production of hard mast in each forest patch in the fall preceding trapping. We collected corresponding data on hard mast production for 37 of 61 spring trapping episodes.

To quantify patch and landscape characteristics, forest patches within the Indian Pine landscape were digitized from aerial photographs (1:15000) and the digital map was analyzed. We calculated patch area and perimeter, proximity, nearest-neighbor distance, core area index, and fractal dimension (Tab. 1). Proximity is inversely related to isolation of a forest patch and is the sum of patch area divided by the nearest squared edge-to-edge distances between a neighboring patch and the focal patch, for all neighboring patches within a specified radius of the focal patch. A radius of 1 km was used in our analysis. Core area index is a measure of the ratio of interior to edge habitat, calculated as the percent of the total patch area > 50 m from the patch's edge. Fractal dimension is a measure of shape complexity and is equal to two times the logarithm of patch perimeter divided by the logarithm of patch area. Squared terms for patch area, proximity, and nearest-neighbor distance also were included in the analyses, after centering on mean values to reduce collinearity (NETER et al. 1990). In all analyses, patch and landscape variables were logarithmically transformed to stabilize variances. Two exceptions were core area index, which was square-root transformed, and fractal dimension, which required no transformation.

### Computation of interaction coefficients

The technique of determining competition coefficients from census data using regression techniques was developed by SCHOENER (1974) and CROWELL and PIMM (1976) and has been the sub-

ject of considerable debate (ABRAMSKY et al. 1986; HASTINGS 1987; PIMM 1985; ROSENZWEIG et al. 1985). Recently, FOX and LUO (1996) addressed a shortcoming of the original technique and used perturbation experiments to demonstrate the validity of a modified Schoener-Pimm analysis. LUO et al. (1998) also have applied the technique to identify seasonal fluxes in the intensity of competition between *Rattus luteolus* and *Pseudomys higginsii* in Tasmania. We briefly outline the pertinent statistical procedures below.

The equilibrium population size for species  $i$ ,  $N_i^*$ , can be expressed using the Lotka-Volterra equations for competition,  $N_i^* = K_i + \sum \alpha_{ij} N_j^*$ , where  $K_i$  is the carrying capacity of species  $i$  in the absence of competitors,  $N_j^*$  is the equilibrium population size of species  $j$ , and  $\alpha_{ij}$  is the per capita effect of species  $j$  on the growth rate of species  $i$  ( $i \neq j$ ). For a community at equilibrium, interaction coefficients ( $\alpha_{ij}$ ) can be estimated from population censuses using linear regression.

Under conditions of heterogeneous habitat, variation in density could be due to differences in habitat selection among species. Incorporating the potential effects of  $M$  local habitat variables,  $H_m$ , into a model for predicting the equilibrium density of species  $i$  yields (after HALLETT 1982)  $N_i^* = \beta_0 + \sum \alpha_{ij} N_j^* + \sum \beta_{im} H_m$ . Several methods for computing estimates of  $\alpha_{ij}$  have been proposed for this model. CROWELL and PIMM (1976) used stepwise multiple linear regression performed on principal components for habitat. After habitat components entered the model, densities of other species were allowed to enter the equation. ROSENZWEIG et al. (1984) also used a stepwise regression performed on habitat components as explanatory variables, with density as the response variable. Residuals were saved from each regression, and then a series of regressions were conducted on the residuals, with each species taking its turn as the dependent variable. Both the Crowell-Pimm method and the residual analysis method attempt to estimate interaction coefficients between species after accounting for variation in species densities that can be explained by habitat variables. This is a conservative approach, because some segregation due to habitat may be a result of competitive interactions. ROSENZWEIG et al. (1985) proposed a "free" regression approach in which stepwise regression is conducted on habitat variables and species densities simultaneously, thus permitting species interaction terms to enter the model before habitat components.

Dependence of  $\alpha_{ij}$  estimates on the variances of species densities is a problem of all of the above methods for estimating interaction coefficients. FOX and LUO (1996) addressed this problem by

standardizing density estimates for each species so that mean standardized density equalled 0 and variance equalled 1. They applied this approach to estimate interaction coefficients for a small mammal assemblage in which field removal experiments also were conducted. Interaction coefficients estimated using standardized densities matched coefficients computed from removal experiments quite well (Fox and Luo 1996). Luo et al. (1998) also used standardized densities to obtain reasonable estimates of interaction coefficients for a pair of small mammal species censused across three seasons in Tasmania. Thus, standardized densities should be used instead of unstandardized densities when estimating competitive effects.

In our analysis, we standardized the density estimates so that each species' density had a mean of 0 and a standard deviation of 1. We then used these standardized densities as response variables in stepwise linear regressions ( $F > 2.0$  to enter the model) adhering to the Crowell-Pimm, residual analysis, and free regression methods.

A second problem not addressed by published methods for estimating interaction coefficients is their focus on local habitat selection by species. In light of recent evidence indicating the occurrence of habitat selection at larger spatial scales (LINDENMAYER et al. 1999, 2000; SCHWEIGER et al. 2000), we modified the model of HALLETT (1982) to incorporate the effects of Q patch effects,  $P_q$ , and R landscape-level effects,  $L_r$ , on the density of species  $i$ :

$$N_i^* = \beta_0 + \sum \alpha_{ij} N_j^* + \sum \beta_{im} H_m + \sum \gamma_{iq} P_q + \sum \phi_{ir} L_r$$

We conducted a separate analysis for the complete set of 61 censuses, and for the subset of 37 censuses for which data on hard-mast production also were available. To reduce dimensionality, local habitat, patch, and landscape-level variables were subjected to principal components analysis (PCA). Only scores for principal components with eigenvalues  $> 1$  were used in regression models. In each analysis, we estimated interaction coefficients in the following manner: Two separate regressions were performed for each species of sciurid. In one regression we used as explanatory variables principal components derived only from local habitat variables. In the other regression we used principal components derived from local habitat variables and principal components derived from pooled patch and landscape variables. Our motivation for partitioning the explanatory variables was to determine whether variation in species densities could be explained by variables operating at multiple spatial scales, and to assess the degree to which inclusion of patch and landscape metrics affected estimates of interspecific interaction.

## Results

The 61 spring trapping episodes yielded captures of 1669 white-footed mice, with mice captured in all trapping episodes. In addition, we captured 207 fox squirrels in 43 episodes, 264 eastern chipmunks in 47 episodes, 78 gray squirrels in 14 episodes, and 31 red squirrels in 12 episodes. Trapping in the spring following estimation of hard-mast production at 37 sites yielded captures of 961 white-footed mice at 37 sites, 148 fox squirrels at 29 sites, 147 eastern chipmunks at 28 sites, 46 gray squirrels at 7 sites, and 18 red squirrels at 6 sites. The number of sites at which we caught gray and red squirrels was marginal for use in subsequent regression analysis. Southern flying squirrels (*Glaucomys volans*) were excluded from analysis, as they were captured only in the 2 extensive woodlands and 3 of the largest forest patches.

When all 61 episodes were considered, PCA on the local habitat variables yielded seven usable principal components (i.e., eigenvalues  $> 1$ ), and these components explained 80.2% of the total variation of the original variables. PCA on the patch and landscape-level variables yielded three usable components that together explained 90.3% of the total variation. When the 37 sites with data on mast production were considered separately, PCA on the local habitat variables yielded eight usable components, and these components explained 83.4% of the total variation. PCA on the patch and landscape-level variables yielded three usable components that together explained 84.3% of the total variation.

For each species, we obtained significant regression models relating standardized densities to the principal components derived from local habitat variables. These models explained 9–64% of the variance in standardized density estimates when all trapping episodes were used and 20–60% of the variance when only the 37 episodes with data on hard-mast production were used (Tab. 2). When we constructed regression models using principal components from both local habitat variables and patch and

**Table 2.** Coefficients of multiple determination (adjusted  $R^2$ ) and P values (in parentheses) for regressions relating standardized density to principal components of either local habitat variables alone or in combination with principal components of patch and landscape variables. Separate analyses were conducted for all spring trapping episodes ( $n = 61$ ) and for those episodes for which hard-mast production was estimated the preceding fall ( $n = 37$ ). For white-footed mice, too few trapping episodes occurred at sites  $\geq 10$  ha to permit analysis.

Species	Crowell-Pimm and Residual Analysis Methods		Free Regression Method	
	Local Habitat Only	Local + Patch + Landscape	Local Habitat Only	Local + Patch + Landscape
<b>All Trapping Episodes</b>				
White-footed mice, < 10 ha	0.41 (0.001)	0.41 (0.001)	0.41 (0.001)	0.41 (0.001)
White-footed mice, $\geq 10$ ha	0.64 (0.004)	0.61 (0.012)	0.64 (0.004)	0.61 (0.012)
Eastern chipmunks	0.34 (0.001)	0.46 (0.001)	0.36 (0.001)	0.46 (0.001)
Fox squirrels	0.09 (0.030)	0.09 (0.030)	0.09 (0.030)	0.09 (0.030)
Gray squirrels	0.34 (0.001)	0.45 (0.001)	0.37 (0.001)	0.45 (0.001)
Red squirrels	0.37 (0.001)	0.45 (0.001)	0.37 (0.001)	0.45 (0.001)
<b>Episodes with Mast Data</b>				
White-footed mice, < 10 ha	0.42 (0.005)	0.42 (0.003)	0.42 (0.005)	0.42 (0.003)
Eastern chipmunks	0.35 (0.002)	0.46 (0.001)	0.37 (0.001)	0.46 (0.001)
Fox squirrels	0.20 (0.025)	0.20 (0.025)	0.27 (0.006)	0.30 (0.006)
Gray squirrels	0.54 (0.001)	0.71 (0.001)	0.55 (0.001)	0.74 (0.001)
Red squirrels	0.60 (0.001)	0.63 (0.001)	0.60 (0.001)	0.64 (0.001)

landscape-level variables, substantial increases in adjusted  $R^2$  values occurred for eastern chipmunks (increases of 0.09–0.12) and gray squirrels (increases of 0.08–0.19), moderate improvements in  $R^2$  values were noted for red squirrels (increases of 0.03–0.08), and little or no change in  $R^2$  values occurred for fox squirrels (0.00–0.03) and white-footed mice (–0.03–0.00) (Tab. 2).

Estimates of interaction coefficients generally were similar within a given set of data, irrespective of the regression method used. Generalized community matrices (HALLETT 1982) for interaction coefficients estimated after accounting for components of local habitat indicated significant negative effects of eastern chipmunks on densities of white-footed mice in forest patches  $\geq 10$  ha and reciprocal negative effects between chipmunks and fox squirrels (Tab. 3). When the effects of patch and landscape-level variables were incorporated into the estimation procedure, the negative interactions noted previously with the local habitat variables were retained (Tab. 4). In addition, we noted significant positive effects of mice

and fox squirrels, and a negative effect of gray squirrels, on density of red squirrels (Tab. 4).

## Discussion

Because of the importance of patch and landscape features to density of some of the species in our assemblage, estimation of competitive interactions should account for variation in density due to habitat features measured at multiple spatial scales. Of the five species we examined, gray squirrels and eastern chipmunks are the most sensitive with respect to habitat fragmentation (NUPP and SWIHART 1998, 2000), whereas red squirrels, fox squirrels, and white-footed mice appear to be progressively less sensitive (BAYNE and HOBSON 2000; NUPP and SWIHART 1998, 2000; SWIHART and NUPP 1998; GOHEEN and SWIHART unpubl. data). In accord with these differences, models for gray squirrels and eastern chipmunks exhibited the greatest increase in variation explained when patch and land-



**Table 3.** Generalized community matrices for five species of granivorous forest rodents in west-central Indiana, U.S.A. Entries indicate the per capita effect of the column species on the row species, taking into account the effects of local habitat on species density. For a given species pair, interaction coefficients are listed in the following order: Crowell-Pimm, residual analysis, free regression. All interaction coefficients in the table exhibited P values < 0.05.

	White-footed mice	Eastern chipmunks	Fox squirrels	Gray squirrels	Red squirrels
All Trapping Episodes					
White-footed mice					
< 10 ha		-	-	-	-
≥ 10 ha		-0.22	-	-	-
		ns			
		-0.22			
Eastern chipmunks					
			-0.27	-	-
			-0.27		
			-0.28		
Fox squirrels					
	-	-0.26		-	-
		-0.37			
		-0.26			
Gray squirrels					
	-	-	-		-
Red squirrels					
	-	-	-	-	-
Episodes with Mast Data					
White-footed-mice					
< 10 ha		-	-	-	-
Eastern chipmunks					
	-		-0.37	-	-
			-0.38		
			-0.41		
Fox squirrels					
	-	ns		-	-
		-0.44			
		-0.45			
Gray squirrels					
	-	-	-		-
Red squirrels					
	-	-	-	-	-

scape components were included in regressions. Smaller increases in explanatory power were evident for red squirrels when patch and landscape components were included in regression models. For fox squirrels and mice, inclusion of patch and landscape components contributed virtually nothing to the models' explanatory power. Density of white-footed mice actually is inversely related to patch area (NUPP and SWIHART 1996, 2000), indicating a positive response to habitat fragmentation. Habitat factors measured at multiple spatial scales explained a substantial amount of the total variation in species abundances. In contrast, evidence of strong competitive ef-

fects among species of small mammals in our study was relatively sparse; only three out of 24 possible species interactions were consistently significant for each type of model constructed (local habitat variables only; habitat, patch and landscape variables combined). Local habitat affinities and larger-scale responses to agriculturally induced fragmentation of habitat appear to be the principal determinants of community structure in forest patches, with interspecific interactions relegated to a secondary role. SWIHART and NUPP (1998) drew the same conclusion based on spatially explicit simulation models of gray squirrel, fox squirrel, and red squirrel populations.

**Table 4.** Generalized community matrices for five species of granivorous forest rodents in west-central Indiana, U.S.A. Entries indicate the per capita effect of the column species on the row species, taking into account the effects of local habitat, patch, and landscape-level variables on species density. For a given species pair, interaction coefficients are listed in the following order: Crowell-Pimm, residual analysis, free regression. All interaction coefficients in the table exhibited P values < 0.05 except red-gray, which was 0.06.

	White-footed mice	Eastern chipmunks	Fox squirrels	Gray squirrels	Red squirrels
All Trapping Episodes					
White-footed mice					
< 10 ha		-	-	-	-
≥ 10 ha		-0.26	-	-	-
		-0.18			
		-0.22			
Eastern chipmunks	-		-0.24	-	-
			-0.28		
			-0.24		
Fox squirrels		-0.26			
		-0.46			
		-0.26			
Gray squirrels	-	-	-		-
Red squirrels	0.23	-	0.22	-	
	ns		0.24		
	0.23		0.22		
Episodes with Mast Data					
White-footed-mice					
< 10 ha		-	-	-	-
Eastern chipmunks	-		-0.33	-	-
			-0.33		
			-0.36		
Fox squirrels	-	ns		-	-
		-0.50			
		-0.52			
Gray squirrels	-	-	-		-
Red squirrels	-	-	-	ns	
				ns	
				-0.20	

A possible exception to secondary effects of competition was the mutually negative interaction observed between fox squirrels and eastern chipmunks. Both eastern chipmunks and fox squirrels inhabit woodlands throughout the study area (NUPP and SWIHART 2000). This pattern of co-occurrence places them in potential conflict for a common food source, namely hard mast (KOPROWSKI 1994 a; SNYDER 1982). Consistent with this hypothesis, densities of fox squirrels and eastern chipmunks increase in response to principal components of habitat

variables characterizing basal area of hard mast trees and mast production, respectively (NUPP 1997).

A negative effect of eastern chipmunks also was noted on densities of white-footed mice in large (≥ 10 ha) forest tracts. Both of these species occur syntopically throughout the study area (NUPP and SWIHART 2000). However, previous studies have demonstrated that eastern chipmunks are sensitive to fragmentation and exhibit lower survival in small forest fragments than in continuous tracts of forest (HENEIN et al. 1998; NUPP

and SWIHART 1998), potentially leading to local extinctions from fragments (HENDERSON et al. 1985). Thus, competitive effects of eastern chipmunks on white-footed mice may be dependent on patch attributes and landscape context. We observed a negative effect of chipmunks on mice in large forest patches but not in small (< 10 ha) forest patches, a finding consistent with the hypothesis that mice experience release from competition with larger granivores in small forest patches (NUPP and SWIHART 1998, 2000). Competitive release in fragments appears to be common for small mammals with generalist habitat requirements, although social structure may regulate a species' ability to respond to the absence of competing species (DEBINSKI and HOLT 2000).

The relatively minor role of interspecific interactions in determining current population densities does not imply that competition was unimportant in the relatively continuous forest that characterized pre-settlement Indiana. Historical influences often are represented in current distributions of species and are difficult to identify using current observational data (CONNELL 1983; DRAKE 1990; KELT et al. 1995). Local competition also can influence geographic ranges and the composition of regional biotas (BROWN et al. 2000). Fragmentation of Indiana's forest began approximately 150 years ago (PETTY and JACKSON 1966).

Competition could have played an important role in structuring the distribution and abundance of granivorous rodents in the previously unfragmented forest, but it seems likely that deforestation and concomitant reductions in area and increases in isolation of the remaining forest patches have played an increasingly important role in the last century. Our results thus support the notion that observed interactions between two species may be a function of properties intrinsic to the species and, perhaps more importantly, of properties of the landscape in which they co-occur (DANIELSON 1991; DEBINSKI and HOLT 2000).

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## Zusammenfassung

### Abschätzungen zur Konkurrenz von im Wald lebenden Rodentiaspecies in einer fragmentierten Landschaft im mittleren Westen der USA

Viele Wälder im landwirtschaftlich intensiv genutzten mittleren Westen der USA sind stark fragmentiert, und die Kleinsäugerarten der Habitatinseln zeigen eine nicht zufällige Verteilung. Wir haben den Grad der Konkurrenz zwischen fünf Arten von Samen fressenden Waldnagetieren untersucht, um den Einfluß auf die Struktur des lokalen Vorkommens in Waldinseln abzuschätzen. Dazu wurde die Technik der Regressionskalkulationen erweitert, um Landschaftsvariablen zusätzlich zu den Habitatvariablen einzubeziehen. Nachdem die Varianz der Dichte von interessierenden Arten durch lokale Habitatvariablen erklärt wurde, sind signifikante Konkurrenzeffekte für das Artenpaar *Sciurus niger-Tamias striatus* gefunden worden. *T. striatus* hat außerdem eine negative Wirkung auf die Dichte von *Peromyscus leucopus* in Waldinseln, die größer sind als 10 ha. Die Einbeziehung von Patch-Fläche und Landschaftsvariablen erhöht den Erklärungswert der Regression von *T. striatus*

und *S. carolinensis*, zwei Arten, die als sensibel gegenüber Fragmentierung angesehen werden. Auch wenn die Habitatwahl in einem größeren Maßstab einbezogen wurde, zeigten unsere Ergebnisse Konkurrenzeffekte, die vergleichbar waren mit der Analyse, die nur lokale Habitatvariablen beinhaltete. Eine Ausnahme war eine geringe negative Wirkung von *S. carolinensis* auf *Tamiasciurus hudsonicus* nachdem die Habitatwahl auf unterschiedlicher räumlicher Skala einbezogen wurde. Insgesamt hat die interspezifische Konkurrenz nur für drei von den 24 möglichen Interaktionen einen signifikanten Einfluss auf die Dichte. Im Gegensatz dazu haben Habitat und Landschaftsstruktur 0.37–0.71 der Dichtevarianz für alle Arten außer *S. niger* (0.02–0.20) erklärt. Wir diskutieren die Rolle von Konkurrenz und Habitatfragmentierung auf die Koexistenz von Waldsamenfressern.

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